A new species of *Microgale* (Lipotyphla, Tenrecidae) from isolated forest in southwestern Madagascar.

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SYNOPSIS. A new species of *Microgale* is described on the basis of two specimens collected in southwestern Madagascar. This species occurs in the Parc National de Zombitse-Vohibasia at 780 m in dry deciduous forest and in the montane habitat of the nearby Analavelona Forest at 1050 m, characterised by a mixture of eastern (humid) and western (dry) plant species. This new species has several distinct cranial modifications that appear to be adaptations for living in areas with semi-xeric conditions. A considerable amount of data is available from southwestern Madagascar on local climatic changes during the Holocene. The biogeography of this new *Microgale* is examined in light of these environmental vicissitudes.

RÉSUMÉ. Une nouvelle espèce de *Microgale* est décrite sur la base de deux spécimens collectés dans le sud-ouest de Madagascar. Cette espèce est présente dans le Parc National de Zombitse-Vohibasi à 780 m dans les forêts sèches caducifoliées ainsi que dans l'habitat montagneux de la Forêt d'Analavelona à 1050 m, dont les plantes sont une composition d'espèces de l'est (humide) et de l'ouest (sèche). Cette nouvelle espèce présente plusieurs modifications crâniennes distinctes qui semblent être le résultat de l'adaptation à des zones de conditions semi-xérophiles. Des données considérables sont disponibles sur la région du sud-ouest de Madagascar sur les changements climatiques durant le Holocène. La biogéographie de ce nouveau *Microgale* est examinée à la lumière de ces vicissitudes environnementales.

INTRODUCTION

When MacPhee (1987) conducted his revision of the shrew-tenrecs belonging to the genus *Microgale*, little recently collected material was available for study and numerous taxa were represented by unique or small series of specimens, often poorly preserved and/or poorly prepared. MacPhee's work utilized the vast majority of material available in the world's natural history museums, which amounted at that time to about 120 specimens. Over the past decade there has been a renaissance in field zoological studies on Madagascar, often in the context of biological inventories, and a considerable amount of new small mammal material has been obtained. For example, the number of recently obtained *Microgale* specimens is many times greater than that available for MacPhee's revision. This new material provides the means to clarify the relationships among some named taxa, a redefinition of species limits, and the description of several new species (Jenkins 1992, 1993; Jenkins *et al.*, 1996, 1997; Goodman and Jenkins, 1998).

During field missions in southwestern Madagascar to the Vohibasia Forest in early 1996 and another to the Analavelona Forest in early 1998 single individuals of a shrew tenrec were captured that, after comparison with the literature and reference collections at several museums, could not be identified to species. Even though the animal is known currently only from two specimens, one of which lacks an associated skull, we feel that its unique pelage and cranial features clearly distinguish it from known taxa and a description is provided below.

MATERIALS AND METHODS

All measurements are in millimeters (mm), with the exception of weight which is in grams (g). Standard external measurements were taken in the field and are defined as follows:

Ear length (E): notch at base of ear to the distalmost edge of the pinna.

Head and body length (HB): tip of the nose to the distalmost point of the body (at base of tail).

Hind foot length (HF): heel to tip of the longest toe (excluding claw).

Tail length (TL): base of tail (at right angles to the body) to end of distal-most vertebra, excluding terminal hair tuft.

Weight (Wt): taken with a Pesola spring balance to the nearest 0.5 grams (g).

Cranial measurements were taken using digital calipers or using a microscope measuring stage. Cranial nomenclature follows that of McDowell (1958), Meester (1963) and MacPhee (1981); dental nomenclature that of Mills (1966), Swindler (1976), Butler and Greenwood (1979), and MacPhee (1987). Dental notations are given in the text in the following manner, with premaxillary and maxillary teeth denoted by upper case, mandibular teeth by lower case: incisor (I/i), canine (C/c), premolar (P/p), molar (M/m); thus i3 refers to the third lower incisor.
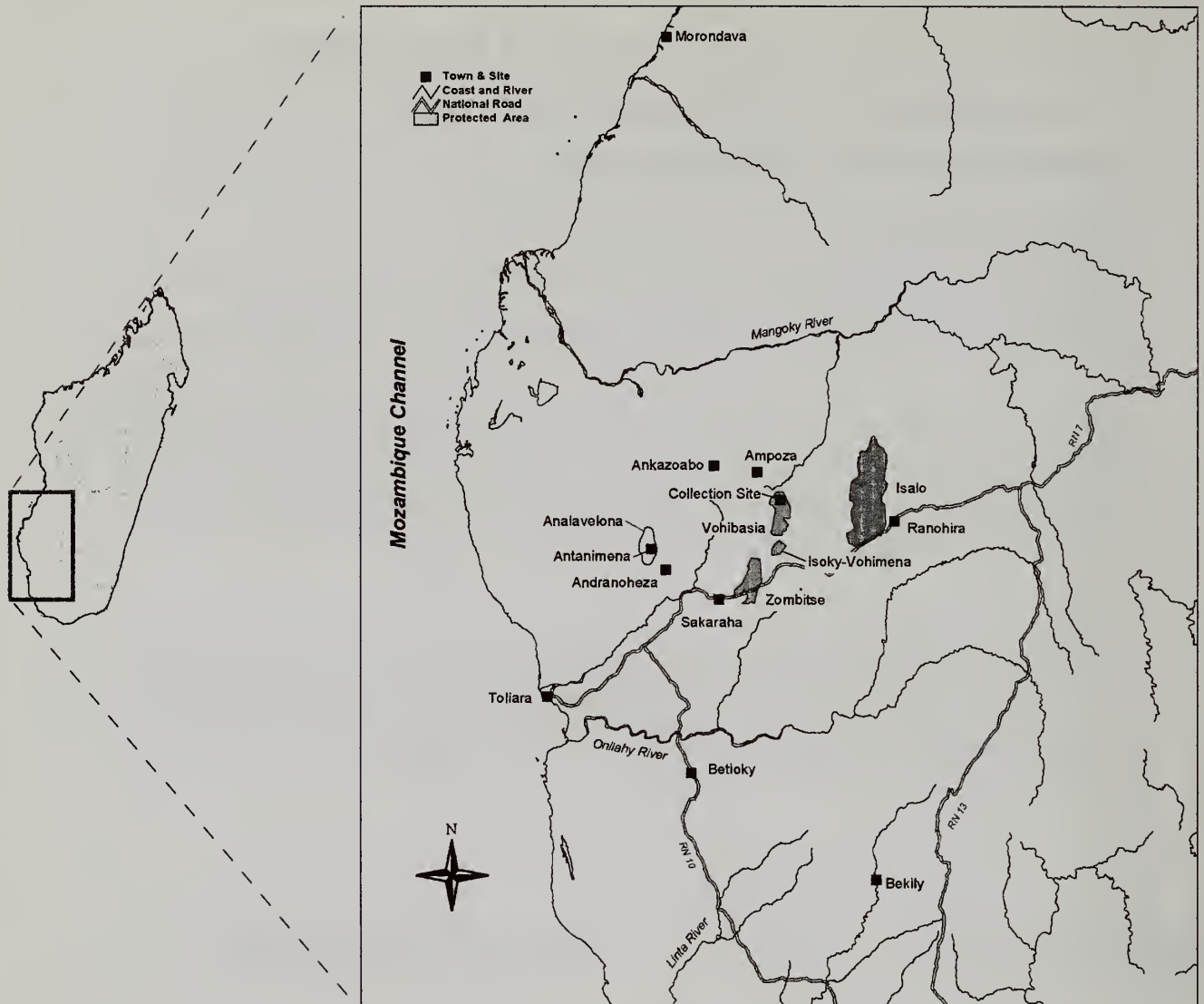
Fig. 1   Map of southwestern Madagascar showing the positions of the Vohibasia and Analavelona forests, as well as other sites mentioned in the text.

RESULTS

Microgale nasoloi sp. nov.

Figs 2–4, 7

HOLOTYPE.   FMNH 156187, field number SMG–7875, adult female, skin, skull and skeleton. Collected by S. M. Goodman and R. Rasoloarison on 12 January 1996. The specimen is deposited in the Field Museum of Natural History, Chicago.

TYPE LOCALITY.   Vohibasia Forest [Forêt de Vohibasia], 59 km northeast of Sakaraha, Province de Toliara, southwestern Madagascar, 22°27.5'S, 44°50.5'E, 780 m, in transitional dry deciduous forest.

REFERRED MATERIAL.   FMNH 161575, field number SMG–10,230,

juvenile male, skin [skull and skeleton lost]. Collected by S. M. Goodman on 14 March 1998 in the Analavelona Forest [Forêt d'Analavelona], near Antanimena, 12.5 km northwest of Andranoheza, 22°40.7'S, 44°11.5'E, 1050 m, on an isolated massif with elements of eastern (humid) and western (deciduous) forests. The specimen is currently at the Field Museum of Natural History and will be repatriated to the Département de Biologie Animale, Université d'Antananarivo, Antananarivo.

DIAGNOSIS.   Pelage grey. Interorbital region constricted; braincase shallow; ectotympanic posteriorly positioned; tympanic processes of alisphenoid and basisphenoid reduced. Roots of P2 adpressed; M3 anteroposteriorly compressed, bucco-lingually elongated; p3 scarcely greater in size than p2.

DESCRIPTION.   Based on holotype unless otherwise stated. Medium sized *Microgale* (see Table 1), superficially mouse-like in appearance (see Figs 2 and 7), tail thin, well-clothed with long scale

Table 1   Selected dimensions of the holotype and paratype of *Microgale nasoloi* compared with adult specimens of *M. cowani* and *M. brevicaudata*. Data is presented as mean ± standard deviation, followed by range, with sample size in parentheses.

	M. brevicaudata	*M. cowani*	*M. nasoloi* Vohibasia FMNH 156187	*M. nasoloi* Analavelona FMNH 161575
Character				
HB	75.00 ± 4.47	77.78 ± 5.64	81	70
	66–82 (10)	68–85 (12)		
TL	35.64 ± 2.84	65.44 ± 3.00	53	62
	30–41 (11)	61–71 (11)		
HF	12.55 ± 0.49	16.03 ± 0.60	13	14
	12–13 (11)	15–17 (12)		
E	11.82 ± 1.11	14.19 ± 1.42	16	16
	10–13 (11)	12–17 (12)		
Wt	11.0 ± 0.89	13.75 ± 0.90	14.0	5.9
	10–12.5 (6)	12.5–15.5 (8)		
Condylo-incisive length	20.87 ± 0.66	22.38 ± 0.44	23.2	
	19.9–22.0 (12)	21.4–23.0 (12)		
Upper toothrow length	9.31 ± 0.33	10.73 ± 0.19	10.2	
	8.7–10.0 (12)	10.4–11.0 (12)		
Rostral breadth	3.53 ± 0.16	2.47 ± 0.85	3.1	
	3.3–3.8 (12)	2.3–2.6 (12)		
Interorbital breadth	5.10 ± 0.14	5.23 ± 0.15	4.3	
	4.9–5.4 (12)	5.0–5.6 (12)		
Braincase breadth	8.83 ± 0.25	10.07 ± 0.18	9.2	
	8.5–9.2 (12)	9.8–10.3 (12)		
Braincase height	5.66 ± 0.18	6.59 ± 0.14	4.9	
	5.4–6.1 (12)	6.4–6.8 (12)		

hairs, shorter than head and body (TL: HB 0.65). Pinnae large and prominent, eyes moderately large. Hindfoot relatively short (HF: HB 0.16). First digit of hindfoot just reaches base of second digit, third digit longest, second and fourth subequal, both slightly longer than fifth. Pelage soft and fine in texture, grey dorsally, grading into darker grey ventrally; manus and pes light buffy grey; lateral portion of rostrum from nose to eyes brown; tail grey, slightly darker above than below, well-clothed with long scale-hairs. Hairs of dorsal pelage grey basally, with pale buffy grey tips, intermixed with guard hairs with grey bases, brown tops and light grey tips. Ventral pelage with grey bases and buffy grey tips. The Analavelona specimen differs slightly in the more pronounced buffy wash on the postero-dorsal and ventral surfaces. Mammary formula: axial 1, abdominal 2, inguinal 1.

Skull medium in length (for dimensions see Table 1) but flattened in appearance and with a narrowly constricted interorbital region (see Fig. 3). Rostrum broad, parallel-sided; interorbital region shallow, long, very narrow and markedly concave; braincase shallow and long, with angular supra-articular facets; lambdoid crest well developed; occipital short, vertically inclined relative to long axis of skull; sinus canal shallowly curved; right and left upper toothrows from I1 to P2 sub-parallel; anterior incisive foramina very large, posterior incisive foramina lie between anterior region of canines; mesopterygoid region long and narrow; mesopterygoid fossa postero-ventrally constricted by markedly inwardly curved pterygoid processes; mandibular fossa broad and shallowly curved; tympanic processes of alisphenoid and basisphenoid very reduced, rostral tympanic process of petrosal reduced; ectotympanic occupies posterior position within tympanic region, not in contact with entoglenoid process of squamosal, tympanic process of alisphenoid or tympanic process of basisphenoid. Mandible moderately robust; coronoid process broad; angular process short and slender but dorsal surface flattened and broad; ascending ramus robust with large dorsal and

ventral articular facets; distance between angular process and ascending ramus short. See Figs 3 and 4 for illustrations of the dentition. First upper incisor (I1) robust, pro-odont, greater in crown height than C, distostyle well developed; short diastema between I1 and I2; I2 robust, approximately equal in crown height to C, anterior accessory cusp and distostyle well developed; I3 small, anteroflexed, slightly taller than distostyle of I2, with which it is in contact; C robust, with small anterior accessory cusp and distostyle; P2 small, slightly greater in crown height than distostyle of C, with which it is in contact, tooth with two closely adpressed roots; P3 small, slightly greater in crown height than I3, protostyle well developed, anterior ectostyle and distotyle present, talon reduced; P4 large, mesostyle, anterior ectostyle and distostyle well developed, talon well developed, especially protocone; well developed, bucco-lingually elongated talons also present on M1 to M3; M3 anteroposteriorly compressed, bucco-lingually elongated. First lower incisor (i1) large, subequal in crown height to i2, hypoconulid (posterior accessory cuspid) well developed; i2 robust, slightly greater in crown height than c, hypoconulid well developed; i3 small, slightly greater in crown height than hypoconulid of i2; c moderately robust, no anterior accessory cuspid, hypoconulid present; p2 small, subequal in crown height to i3, two roots present; p3 small, slightly greater in crown height than p2, with small paraconid and hypoconid; p4, m1 and m2 as in other species of *Microgale*; m3 talonid with low hypoconid, oblique crest and hypoconulid, and shallow talonid basin.

DISTRIBUTION.   Known only from the forests of Vohibasia and Analavelona in southwestern Madagascar between 780 and 1050 m (Figure 1).

ETYMOLOGY.   This new species is named in honor of the late Nasolo Rakotoarison who was Curator of Mammals at Parc Botanique et Zoologique de Tsimbazaza, Antananarivo. Nasolo was

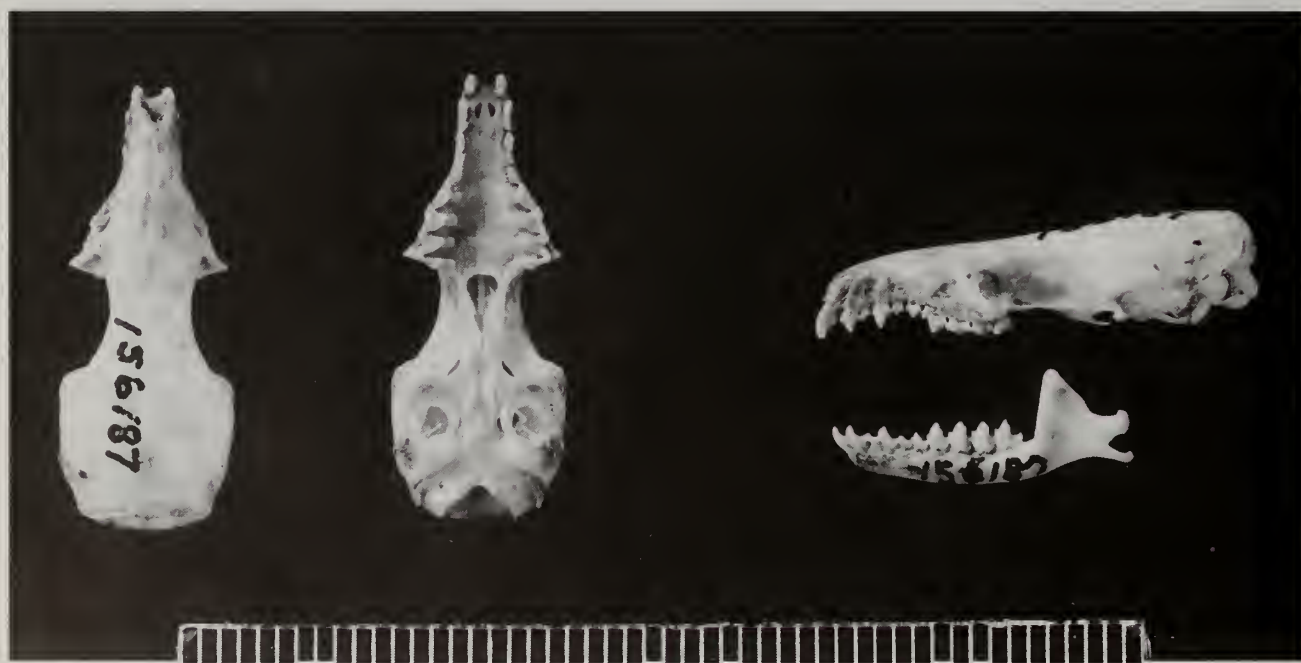**Fig. 2**   Dorsal view of skin of *Microgale nasoloi* (FMNH 156187).

Fig. 3   Dorsal and ventral view of skull, lateral view of skull and mandible of *Microgale nasoloi* (FMNH 156187).
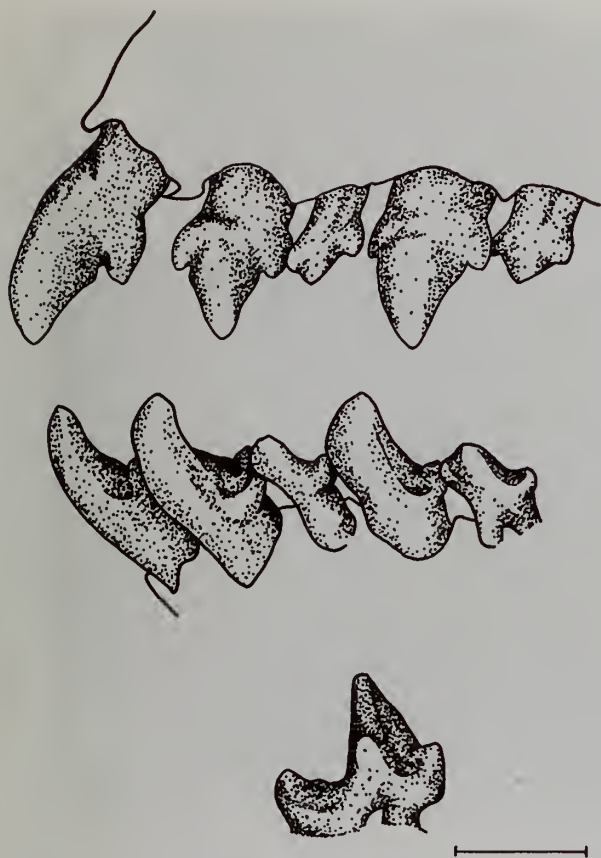
Fig. 4 Dentition of *Microgale nasoloi* (FMNH 156187). Buccal view of left I1 – P2 (above), buccal view of left i1 – p2 (middle), lingual view of left m3 (below). Scale = 1 mm.

passionately interested in mammals and a keen scientist and naturalist.

COMPARISON WITH OTHER SPECIES. Externally *Microgale nasoloi* is readily distinguished from all other species of *Microgale* by the distinctive soft, grey pelage. While it is similar in body size to other medium sized species such as *M. cowani* Thomas, 1882, *M. taiva* Major, 1896a, and *M. drouhardi* G. Grandidier, 1934, larger specimens of *M. fotsifotsy* Jenkins *et al.*, 1997 (for dimensions see Jenkins *et al.*, 1996, 1997) and *M. brevicaudata* G. Grandidier, 1899, the thin, relatively short tail, serves to distinguish it from all of these species with the possible exceptions of *M. brevicaudata* and *M. cowani*. In the case of the latter two species, *M. brevicaudata* has a shorter tail relative to head and body and skull length than *M. nasoloi*, while *M. cowani* has a relatively longer tail (ratio of TL: condylo-incisive length 1.47–1.85 mean 1.70 SD 0.11 n = 10 in *M. brevicaudata*; 2.28 in *M. nasoloi*; 2.7–3.1 mean 3.0 SD 0.13 n = 10 in *M. cowani*).

Microgale nasoloi differs from all other species of *Microgale* in its cranial morphology, particularly the flattened appearance of the skull, in which the shallow braincase is scarcely deeper than the rostrum, the long and very constricted interorbital region and the reduction of some elements of the auditory region. The presence of a well-marked lambdoid crest is a feature shared with *M. brevicaudata* and, to a greater degree, *M. dobsoni* Thomas, 1884 and *M. talazaci* Major, 1896b. The long interorbital region, angular braincase with prominent supra-articular facets and short vertically inclined oc-

ciput of the new species also resembles the condition in *M. dobsoni* and *M. talazaci*.

Microgale nasoloi shows slight similarities in dentition to *M. fotsifotsy* and *M. soricoides* Jenkins, 1993. In *M. nasoloi* I1 is less robust and less pro-odont than that of *M. soricoides*, but more so than in *M. fotsifotsy* and much more so than in other species of *Microgale*; I2 is scarcely smaller than C in *M. nasoloi* and *M. soricoides*; I3 is very small relative to I2 in *M. soricoides*, small in *M. nasoloi* and *M. fotsifotsy*; C is robust but short in crown height as in *M. soricoides*; P2 is small and P3 notably smaller than P4, unlike species of *Microgale* other than *M. dobsoni* and *M. talazaci*. *Microgale nasoloi* differs from other species of *Microgale* in its bucco-lingually elongated talons of P4 to M3, and anteroposteriorly compressed, bucco-lingually elongated M3. Relative sizes of the teeth of the lower anterior dentition are similar to that of *M. fotsifotsy*, with i1 and i2 subequal in crown height and i3 small, unlike *M. soricoides* which has i1 larger than i2.

Preliminary biomolecular analysis provides strong support for a sister relationship between *M. nasoloi* and *M. fotsifotsy* and equally strong support for their sister relationship with *M. soricoides* (Olson, personal communication).

DISCUSSION

Ecology

Vohibasia (15,500 ha) is part of a complex of isolated forest blocks that include Zombitse (14,200 ha) and several smaller satellite forests (see Fig. 1; these surface area estimates are based on 1991 aerial photographs (Langrand and Goodman, 1997). These forests are floristically transitional between eastern humid forest and western dry deciduous forest (Morat, 1973; Du Puy *et al.*, 1994), yet structurally they are closer to dry deciduous forest than humid forest (Fig. 5). Other than these isolated fragments, which were once contiguous, little remains of this transitional forest habitat in southwestern Madagascar, largely as a result of clearing and burning forest for cattle pasture (Salomon, 1993). In 1998, these two forest blocks and the smaller satellite site of the Isoky-Vohimena Forest, were declared as a new reserve known as the Parc National (PN) de Zombitse-Vohibasia.

The Vohibasia Forest generally has a relatively dense understorey, that may at least in part be the result of regeneration after selective removal of hardwoods a few decades ago. Average tree height is less than 10 m (Pétignat *et al.*, 1997). In general the woody vegetation is not particularly spiny in comparison to sub-arid thorn scrub (spiny bush) slightly further west and south. The soils are fine alluvial sands from the Isalo Formation, surface water is highly seasonal, and there is generally little or no soil humus.

The vertebrate communities inhabiting the Zombitse-Vohibasia forests are apparently typical of those found in other arid regions. The known small mammal community consists of five tenrecid lipotyphlans (*Tenrec ecaudatus* Schreber, 1778, *Setifer setosus* (Schreber, 1778), *Echinops telfairi* Martin, 1838, *Microgale nasoloi* and *Geogale aurita* Milne Edwards & G. Grandidier, 1872), one soricid (*Suncus madagascariensis* [Coquerel, 1848]), two exotic murine rodents (*Rattus rattus* [Linnaeus, 1758] and *Mus musculus* Linnaeus, 1758) and two nesomyine rodents (*Eliurus myoxinus* Milne Edwards, 1885 and *Macrotarsomys bastardi* Milne Edwards & G. Grandidier, 1898) (Goodman & Ganzhorn, 1994; Goodman & Rasoloarison, 1997).

To the west of the Zombitse-Vohibasia Forest, a region characterised by a dry climate and distinct deciduous vegetation, is the

Fig. 5   View down old road in the Vohibasia Forest that was cut for geological exploration. Note the relatively dense understorey and sandy soils lacking leaf litter or humus. The trapping site of *Microgale nasoloi* was to the right of the road and about 10 m into the forest. (Photograph by S. M. Goodman).

isolated mountain of Analavelona rising to over 1300 m (FTM, 1979). On the basis of earlier botanical classifications, Humbert & Cours Darne (1965) described the upper zone of the Analavelona Forest as low sclerophyllous forest ('Forêt basse sclérophylle'), surrounding areas of low-lying forests to the east (e.g. Zombitse-Vohibasia) as dry dense forest ('forêt dense sèche') and to the west as Didiereaceae and *Euphorbia* bush ('Didièréacées et Euphorbia haut fourré'). The nearest low sclerophyllous forest to the Analavelona Massif is in the Isalo range, about 110 km to the east. Thus, according to this classification the massif holds a different flora from the immediately surrounding forests.

On the eastern side of the Analavelona Massif the foothills start at about 600 m, and the lower limit of the forest is at about 1000 m and runs to the upper reaches of the mountain. On the basis of botanical research conducted in this forest by Nathalie Messmer and Pierre Jules Rakotomalaza during the March 1998 expedition to the site, in the lower altitudinal portion of the forest massive emergent *Ficus* and *Eugenia* trees with diameter at breast height of 95–110 cm reach heights of up to 25 m. The generic composition of these forest trees indicate that the site is a mixture of eastern humid and western deciduous forest. Considerable ground humus and leaf litter and some epiphytic plants are present, the understorey is open and small streams drain the steep hills. These characteristics are unlike sclerophyllous forest, therefore the classification presented by Humbert & Cours Darne (1965) for Analavelona is inaccurate, although it is possible that the final summital ridge of the mountain is dominated by sclerophyllous plants. On the basis of numerous phytological characteristics the portion of the forest that we visited

is much closer to Humbert & Cours Darne's mid-elevation humid forest ('types humides, moyenne altitude (800–1300 m)'). In summary, the forested portion of the Analavelona Massif is heterogenous with regards to vegetative structure, particularly differences between the western and eastern slopes (Koechlin *et al.*, 1974).

The Analavelona Massif is distinctly moister than any other region of southwestern Madagascar that we are aware of, including portions of the Isalo Massif. Presumably on the basis of orographic position, Analavelona receives regular and considerable precipitation and even during the dry season the summital zone is often shrouded in mist. The extant fauna and flora contain elements that indicate that this site may be a refuge for biota that had much more extensive distributions in southwestern Madagascar when this region was moister in the relatively recent geological past (Raxworthy and Nussbaum, 1997; Goodman, unpublished). The known small mammal community of Analavelona is relatively depauperate and consists of three tenrecid lipotyphlans (*Tenrec ecaudatus, Echinops telfairi* and *Microgale nasoloi*), one soricid (*Suncus madagascariensis*), one introduced murine rodent (*Rattus rattus*) and one nesomyine rodent (*Eliurus myoxinus*) (Goodman, unpublished).

Trapping

Generally on Madagascar, pit-fall buckets have produced good results in capturing ground-dwelling vertebrates, particularly reptiles, amphibians, and lipotyphlans (Raxworthy & Nussbaum, 1994; Goodman *et al.*, 1996). During the April 1993 mission to the Zombitse Forest 528 pit-fall bucket days were amassed; in January 1996 in the Vohibasia Forest, 165 pit-fall bucket days; and in March

1998 in the Analavelona Forest, 198 pit-fall bucket days (Raxworthy et al., 1994; Goodman & Rasoloarison, 1997; Goodman, unpublished). During the same periods, a combination of Sherman and National Live traps were used for a total of 1,088 trap nights in the Zombitse Forest, 955 trap nights in the Vohibasia Forest, and 535 trap nights in the Analavelona Forest. The only individual of *M. nasoloi* taken in one of these devices in the Vohibasia Forest was in a Sherman Live trap baited with a mixture of peanut butter and ground corn flour placed about 1.5 m off the ground, and set about 10 m into the forest from the edge of an old road surrounded by forest habitat. The single individual of this species obtained in the Analavelona Forest was in a pit-fall device placed within 25 m of the forest edge. Given the general efficiency of these two trapping techniques in capturing a wide variety of non-volant small mammals, including terrestrial and semi-arboreal lipotyphlans, it appears that *M. nasoloi* is uncommon or difficult to trap with these devices.

Presumably this species also occurs in at least the nearby Zombitse Forest and perhaps other smaller forest satellites that until their recent fragmentation were part of an extensive area of transitional forest. It was not found in the Isoky-Vohimena Forest (22°41.0'S, 44°49.8'E), lying between Zombitse and the PN de l'Isalo which was inventoried in late January 1996.

Natural history

The lipotyphlan fauna of Madagascar is much more diverse in humid areas of the island and only a few species have been recorded in the drier west and southwest. Other than those species mentioned above for the Zombitse-Vohibasia and Analavelona forests, three others have been reported in dry areas of the island. *Microgale brevicaudata* is known from the northwest possibly as far south as Morondava or Toliara (MacPhee, 1987; Raxworthy & Nussbaum, 1994; Ganzhorn et al., 1996); *M. pusilla* Major, 1896a from the Mahafaly Plateau in the extreme southwest, although this material recovered from owl pellets may date from a period in recent geological times when this region was more mesic (MacPhee, 1986); and a long-tailed *Microgale* associated with the *longicaudata* group from near Morondava (Ade, 1996).

Little biological data may be gleaned from the capture of the two individuals of *M. nasoloi*. The Vohibasia animal was a pregnant female with two embryos in the left and one in the right oviduct; the embryos measuring 10 mm in crown to rump length. On the basis of embryo size, the female was near parturition at the time of capture in mid-January. In contrast to the data available for species of *Microgale* recorded from eastern humid forest, no quantitative information on the reproductive season of small lipotyphlans is available from the southwestern portion of the island. Nevertheless, given that in the eastern humid forest a considerable number of *Microgale* species give birth during the early portion of the rainy season, which normally commences in late November and early December, a mid-January date for parturition would coincide with the beginning of the rainy season in southwestern Madagascar which tends to occur later than in the east (Donque, 1975).

The individual from Analavelona was a male with small abdominal testes measuring 3×2 mm and non-convoluted epididymides. Unfortunately, the skull is not available to assess the age of the individual using dental characters, but on the basis of reproductive condition this animal was probably a juvenile. Further evidence to support this supposition is that the male is smaller than the adult female in several external measurements and body mass, all characters that tend to vary with age. The pit-fall bucket in which the male was captured contained the chewed remnants of beetles and cockroaches, which it presumably fed upon before being removed from the trap.

The Vohibasia specimen was trapped 1.5 m above the ground on a vine running from the soil surface to the mid-canopy at an angle of about 15° (Fig. 6), suggesting that it must be at least competent at scrambling along supports. Anatomically however, it does not exhibit the features normally associated with arboreality in other members of the genus, since the relatively short tail and hindfoot suggest a greater affinity for a mainly terrestrial lifestyle. In the most extreme cases, *M. longicaudata* Thomas, 1882 and *M. principula* Thomas, 1926 have very long, naked-tipped tails approximately twice as long as head and body length, long hindfeet, and are demonstrably able to make use of slender supports above the ground (Goodman & Jenkins, 1998). Caution should be exercised in attributing morphological adaptations to particular lifestyles, since *Echinops*, which lacks an external tail is nevertheless an adept climber.

The thesis expounded by Eisenberg & Gould (1970), that species of *Microgale* may be divided into different locomotory classes based on differences in tail and hindfoot length relative to head and body length, was criticised by MacPhee (1987) because of lack of ecological evidence. Recent direct observation, plus mainly circumstantial evidence from trap locations, suggest that many species of *Microgale* are generalists equally at home on the ground as scrambling amongst lower levels of the understorey; while a few also use additional ecological niches, such as the long-tailed *M. longicaudata* and *M. principula* which are adept at exploiting thinner supports above ground level.

Microgale nasoloi exhibits some features – pale pelage, prominent pinnae, short hindfoot relative to head and body length, skull with a broad bimaxillary region, narrow interorbital constriction, flat and broad braincase with pronounced superior articular facets and marked lambdoid crest, well developed anterior dentition and anteroposteriorly compressed M3 – which in combination are unique to this species of *Microgale*. Many of these features are, however, also present in the Malagasy geogaline tenrec, *Geogale aurita*, while several are reminiscent of the suite of external, cranial and dental characters which Hutterer (1986) used to define *Afrosorex* as a subgenus of *Crocidura* (Lipotyphla: Soricidae). Species assigned to *Afrosorex* inhabit savanna or forest-fringe areas and the pale dorsal pelage coloration and prominent pinnae, shown also by *Geogale* and *M. nasoloi*, are presumably adaptations to semi-xeric conditions. The parallelism in dental features is possibly also an example of similarities in dietary adaptations. One of the other three species of *Microgale* known to occur in dry habitats is *M. brevicaudata*, and this species also shows some features converging on *M. nasoloi*, *Geogale* and *Afrosorex*. Externally all of these taxa have prominent ears and short hindfeet, while all but *M. nasoloi* have a markedly short tail, however *M. brevicaudata* shows none of the craniodental features shared by *M. nasoloi*, *Geogale*, and *Afrosorex*. This suggests that these shared external features are more plastic than the cranial features and are thus more readily influenced by the dry conditions of savanna or forest fringe habitats, or that species such as *M. brevicaudata* have been adapting to dry or to less extreme conditions for a shorter evolutionary period than others such as *M. nasoloi* and *Geogale*.

Biogeography

Just a few kilometers from the Vohibasia Forest there is the paleontological site of Ampoza, which has yielded a remarkable amount of subfossil material that provides insight into environmental change in southwestern Madagascar over the past few millennia. On the basis of current data derived from a pollen core at Andolonomby (75 km SW from Analavelona and 140 km SW from

Fig. 6 Exact position of trap in the Vohibasia Forest that captured the holotype specimen of *Microgale nasoloi*. The trap was placed about 1.5 m off the ground and the trap opening was facing the direction of the canopy and it is most likely that the animal was descending the vine when captured. Note the thick woody understorey of the forest. (Photograph by S. M. Goodman).

Fig. 7 Photograph of the live individual of the holotype of *Microgale nasoloi* (FMNH 156187). (Photograph by J. Durbin).

Vohibasia), these climatic shifts involved a mesic period starting before 5000 years Before Present (BP) and an arid period between 3500 and 2500 years BP (Burney, 1993). These proposed shifts are mirrored in changes of species representation and habitat types of subfossils excavated from sites in southwestern Madagascar (Goodman & Rakotozafy, 1997) including Ampoza (Goodman, in press). Radiocarbon dates available from Ampoza include an AMS date of 1350 ± 60 BP from a bone of *Hypogeomys antimena* A. Grandidier, 1869, an endemic large rodent that no longer occurs in the region (Goodman & Rakotondravony, 1996). Further, bone remains of extinct giant tortoises from the site have been dated to 1910 ± 120 BP (Mahé & Sordat, 1972) and 2035 ± 35 BP (Burleigh & Arnold, 1986). Although these radiocarbon dates are more recent than Burney's proposed period of aridification, the important point for this discussion is that over the past few millennia there has been significant change in the environment of the Vohibasia and Analavelona region as reflected by the fauna.

Over the past few years a number of studies have tried to correlate aspects of the speciation of certain Malagasy vertebrates with vicariant events derived from information on shifts in vegetational communities during the Quaternary. These paleoecological extrapolations are derived almost exclusively from palynological data dating from the Holocene. In many cases several of the hypotheses advanced seem to explain patterns of the distribution of certain taxa, particularly those living in montane zones of the east (Carleton & Goodman, 1996, 1998). A similar argument in the case of *Microgale nasoloi* may be formulated as follows: during the recent geological past when the region was more mesic, the distinctly more humid forest currently restricted to the upper reaches of the Analavelona Massif would have been more extensive, consequently, *M. nasoloi* would have had a broader distribution. As the climate became drier and the humid forest retreated towards the summital area of Analavelona, the distribution of this animal also contracted, leaving remnant populations at sites with suitable habitat to support it, such as the Vohibasia Forest.

For *M. nasoloi* there appears to be a conflict between aspects of morphological adaptations, namely a species adapted to semi-xeric conditions and the above scenario associated with a more mesic Holocene in southwestern Madagascar. Given these adaptations it is possible that the opposite sequence took place – as more mesic forest dominated the landscape this species was pushed into drier areas of the southwestern Madagascar, and only after becoming more arid was it able to colonize or recolonize this region. On the basis of very limited information it appears that this species is forest-dwelling and

currently restricted to the forests of Analavelona and Vohibasia. However no intensive small mammal surveys, particularly with pitfall traps, have been conducted in spiny bush areas of southwestern Madagascar or the PN de l'Isalo and this species might have a much broader distribution than currently known. Analavelona is a form of mist-oasis and almost certainly a Pleistocene (or earlier) refuge for humid forest-dwelling animals (Raxworthy & Nussbaum, 1997), while the Vohibasia Forest shows transitional aspects between the humid forests of the east and the deciduous forests of the west. Given the ecological variation in this region during the Holocene and recent times, a single coherent explanation for the distribution of this species is not obvious. It exists in the most mesic portions of southwestern Madagascar and is unknown from spiny bush. Perhaps during historical periods when there was more forest cover in the region its distribution was more widespread.

In recent years several studies have examined the phylogeny of reputed Malagasy vertebrate adaptive radiations, often using biochemical characters. Using models of genetic clocks these studies indicate that much of the mammalian intrageneric speciation took place during the Pliocene (Jansa *et al.*, in press). No information is available on the paleoecology of southwestern Madagascar dating from the Pliocene and most of the Pleistocene. If indeed the period in which *Microgale nasoloi* speciated falls within this same epoch and was the result of some vicariant event such as a shift in vegetational structure, we are currently unable to propose models to put its modern distribution into any geographical context.

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